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Avian responses to 25 years of eastern hemlock (*Tsuga canadensis*) decline in the southern Appalachian Mountains

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ABSTRACT

Nonnative invasive pests on forest trees can have profound impacts on wildlife habitat quality and conservation through changes in forest structure and composition that accompany tree mortality. The eastern hemlock (*Tsuga canadensis*), a foundation forest tree species in eastern North America, is highly susceptible to the invasive hemlock woolly adelgid (HWA). In the southern Appalachian Mountains, despite lower hemlock density than further north, mortality from HWA has been particularly fast, likely due to warmer winter temperatures. We sought to understand the impacts of hemlock decline on forest birds in the Great Smoky Mountains National Park in southeastern North America, and how these impacts compared to those from other studies across the hemlock range. We compared pre- and post-HWA avian point count data at 200 sites, and used community-level, relative abundance, and occupancy analyses to understand changes for bird species and communities after 25 years of hemlock decline. We found relative abundance declines in many hemlock-associated bird species as expected, and that avian community composition post-HWA was less structured by hemlock basal area. Bird species with hemlock-associated occupancy declines likely responded to forest structural changes, including loss of forest canopy and increased understory density. We found both similarities and differences between our results and those from other bird-hemlock studies and suggest that these differences may be due to geographic differences in both initial hemlock density and forest succession following loss. Our findings confirm that continued treatment for HWA remains an important tool for the conservation of hemlock trees and associated wildlife habitat conditions.

1. Introduction

The eastern hemlock (*Tsuga canadensis*) is a foundation forest tree species throughout its range in eastern North America (Yamasaki et al., 2000; Ellison et al., 2005), spanning from southern Canada to northern Georgia and west through the central Great Lake states. This evergreen conifer is a shade-tolerant, long-lived, late successional species that regulates streamflow and nutrient cycling of forest soils (Brantley et al., 2013, 2015). The unique structure and dense foliage of hemlocks provide shaded microclimates and support an array of wildlife, from mammals to salamanders and arthropods (Ellison et al., 2018; Thomas and Orwig, 2025). Bird-hemlock associations are a particularly well-studied phenomenon across the hemlock range (Yamasaki et al., 2000). Unlike most needle-leaved trees, healthy hemlocks retain their lower branches, providing habitat for foraging, nesting, and roosting (Vose et al., 2013; Toenies et al., 2018).

Eastern hemlock (hereafter "hemlock") and the southern Appalachian endemic Carolina Hemlock (*T. caroliniana*) are highly susceptible to the invasive Hemlock woolly adelgid (HWA; *Adelges tsugae* Annand), often leading to mortality in as little as four years after infestation (Krapfl et al., 2011). Discovered in Virginia in the 1950s, HWA has spread through much of the range of hemlocks (Fig. 1) causing widespread declines and mortality, and hemlock life history traits make it slow to recover from such events (Ellison et al., 2018). Although HWA initially infested hemlocks in the Northeast much earlier than in the Southeast, hemlock decline occurred much more rapidly in the southern

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Appalachians, probably due to milder winter temperatures that facilitated HWA survival and dispersal (Skinner et al., 2003; Ford and Vose, 2007). This, coupled with a drought in the early 2000s, led to widespread and rapid hemlock loss in the Great Smoky Mountains National Park (GRSM) (Ford et al., 2012).

Avian community composition and diversity have changed in response to hemlock loss according to several studies from the northeastern part of its range (Fig. 1; Tingley et al., 2002, Ross et al., 2004, Becker et al., 2008, Amaral et al., 2023), but less is known about avian responses to hemlock decline in the Southeastern United States. Improved understanding of geographic variation in avian responses to hemlock loss could have conservation and management implications, potentially suggesting regionally appropriate approaches to habitat management for hemlock-associated birds (Amaral et al., 2023).

Though hemlock can form nearly monotypic stands across much of its northeastern range, it is considered a co-dominant to a minor constituent of forests in the southern Appalachians (Block et al., 2012), which harbor higher floristic diversity in general (Manos and Meireles, 2015). Found here in mixed riparian zones and rich coves (Ellison et al., 2005), hemlock dominates only on steep, higher-elevation mesic slopes (Whittaker, 1956). Because the timing and severity of hemlock loss depends on both initial hemlock density and environmental conditions, the ecological consequences can vary geographically. The large canopy gaps created by hemlock die-offs allow for increases in secondary growth, with hardwood regeneration more common in the Northeast but increases in evergreen shrubs like rhododendron (*Rhododendron maximum*) more common in the Southeast (Ford et al., 2012; Webster et al., 2012; Dharmadi et al., 2019). Further, because of the riparian nature of hemlocks in the Southeast, impacts to hydrological processes may be greater than further north (Brantley et al., 2013). Impacts of HWA on nitrogen mineralization rates, however, were found to be minor in southern Appalachian forests that typically contain less than 50% hemlock basal area (Knoepp et al., 2011), and the impact of hemlock loss on nitrogen retention was more severe in the Northeast compared to the southern Appalachians (Block et al., 2012). Whether geographic differences in HWA-driven forest change similarly drive variation in avian responses to hemlock loss remains unclear.

Despite the relative lack of pure hemlock stands in the southern

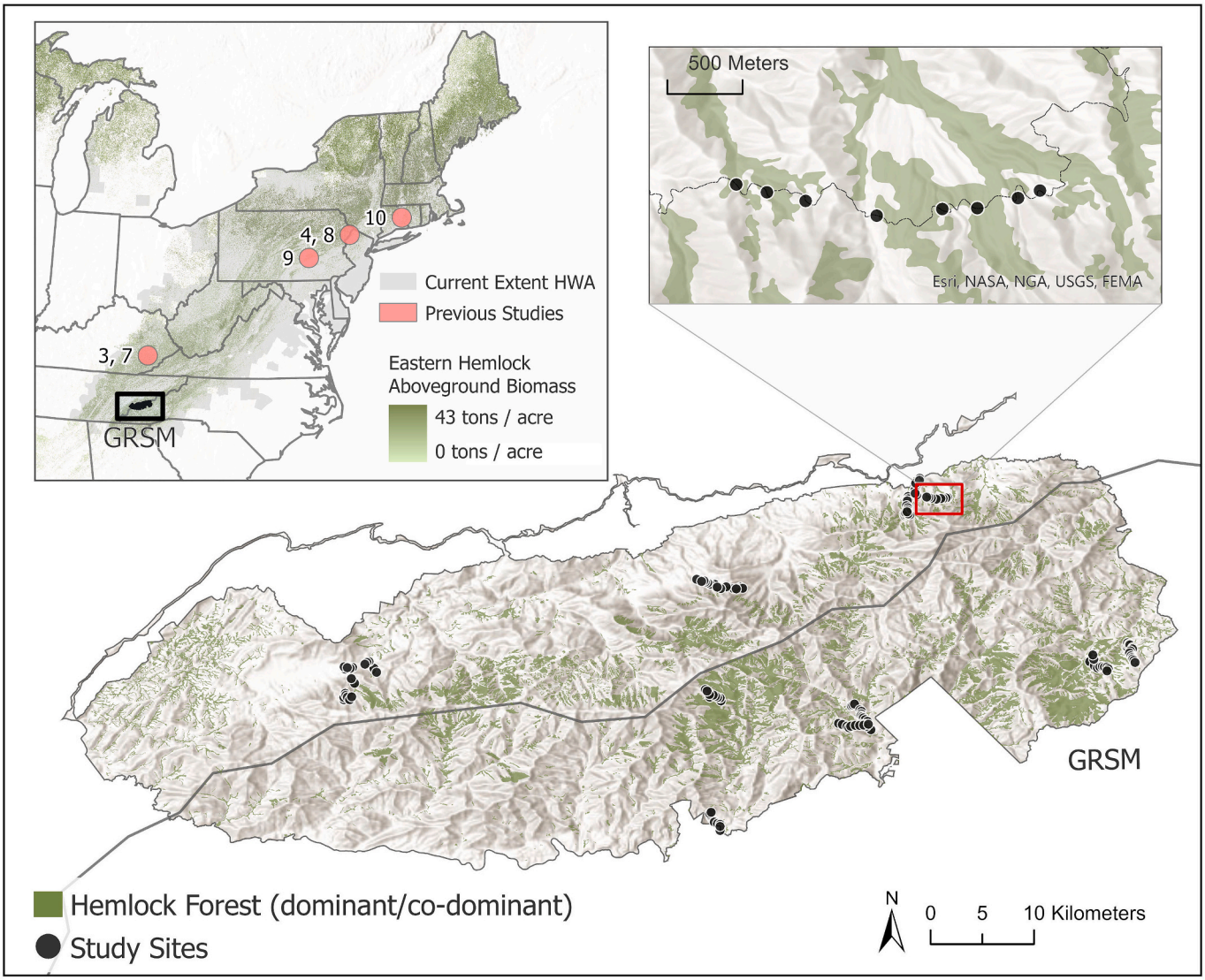


Fig. 1. GRSM, with shaded topographical profile, a green forest type layer where eastern hemlock was dominant or co-dominant, and our 200 study sites, with an inset showing sites spaced at least 250 m apart along trails (National Park Service - Great Smoky Mountains National Park, 2025). FIA BIGMAP Tree Species Aboveground Biomass from Wilson et al. (2018), with sites of previous bird-hemlock studies and numbers as referenced in Fig. 6. HWA distribution as of 2024 from USDA Forest Service (Hemlock Woolly Adelgid National Initiative, n.d.). Note these data are clipped at the United States-Canada border; the distributions of eastern hemlock and HWA extend northward. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Appalachians, it was the second most common tree species in a large-scale vegetation survey conducted by Simons et al. (2006) in GRSM. Simons et al. (2006) also found positive hemlock associations among more than half of the thirty most common breeding birds detected there. Several neotropical migratory species, including Blue-headed Vireo (*Vireo solitarius*), Black-throated Blue Warbler (*Setophaga caerulescens*), and Blackburnian Warbler (*S. fusca*) show close associations with hemlocks in studies from further north (Ross et al., 2004; Toenies et al., 2018), and have suffered declines with hemlock loss. In the Northeast where hemlock is a dominant species, Tingley et al. (2002) found that Black-throated Green Warbler (*S. virens*) abundance declined by 93% when comparing low and high hemlock decline sites, and that there was a negative correlation between hemlock mortality and the abundance of several other neotropical migrants.

The objective of our study was to evaluate changes in avian relative abundance and occupancy associated with hemlock decline in GRSM, near the southern extreme of the hemlock range (Fig. 1). We compared historical bird survey data collected before the introduction of HWA to GRSM with recent bird surveys at the same study sites, using a combination of community-level approaches and species-level dynamic occupancy analyses. We hypothesized that many of the same bird species negatively impacted by hemlock decline in studies from the northern part of the hemlock range would show similar negative trends, and that some disturbance- and secondary growth-associated species would show positive trends where hemlock decline was strongest. Given the regional differences in initial hemlock density and in bird communities, differences in post-HWA plant regeneration, and the length of time between surveys (~25 years post HWA in our study), we expected some aspects of avian response to hemlock decline to differ from those found in more northern parts of the hemlock range. In general, we expected that avian communities would be less structured by the presence of hemlock following 25 years of HWA infestation. We hypothesized that avian diversity and abundance would be reduced at sites showing high hemlock decline, and that bird species associated with hemlock in this southern portion of its range would show negative trends. Additionally, we expected that southeastern species associated with disturbance, secondary growth, and shrubs would show positive trends where hemlock decline was strongest, and species associated with intact forest canopy and open understory conditions would show negative trends. Testing these hypotheses is important to better understand potential geographic differences in bird responses to hemlock decline that would lead to regionally distinctive conservation implications and management decisions.

2. Methods

2.1. Study area and site selection

Spanning over 200,000 ha of nearly contiguous forest, GRSM encompasses parts of western North Carolina and eastern Tennessee and is situated along the southern portion of the Appalachian Mountain Range. GRSM is one of the largest unfragmented forest ecosystems in the southeastern United States and is a global biodiversity hotspot. Complex topography and a wide elevational range (575–2024 m) support a variety of habitat types (Whittaker, 1956), from pine (*Pinus*) – oak (*Quercus*) forests at lower elevations, mixed oak – hickory (*Carya*) and rich cove forests at mid elevations, to Red spruce (*Picea rubens*) – Fraser Fir (*Abies fraseri*) forests at high elevations. Hemlock is considered one of the more common tree species in GRSM (Robert et al., 2009). *Rhododendron maximum* is a common understory to midstory shrub species often found alongside hemlocks in riparian areas (Dudley et al., 2020), and *R. catawbiense* is found at higher elevations, usually in non-forest habitats.

We selected 200 sites within GRSM to conduct avian point count resurveys and measure hemlock condition. All sites were previously surveyed by Shriner (2001) between 1996 and 1999 as part of a large-scale survey of breeding birds and vegetation associations, and we refer to this work as the pre-HWA era. The original 4000 survey sites selected by Shriner (2001) were on low-traffic trails with a mostly closed canopy spaced at least 250 m apart. We filtered these by several criteria to select our sites. These sites needed to include a) a range of historical hemlock abundance from no hemlock to strong historical abundance, as determined by Shriner (2001); b) a range of elevations where hemlocks are found in GRSM; and c) multiple ($\geq$ 2) pre-HWA bird surveys to account for varying detection probabilities. The resulting sites ranged from 538 to 1651 m in elevation, occurred in a variety of forest types (lower elevation riparian, mixed oak/hickory, northern hardwood, and high-elevation spruce/fir), and varied in hemlock dominance and mortality.

Additionally, many hemlocks in GRSM have been systemically treated with the neonicotinoid pesticide imidacloprid (Johnson et al., 2008). We did not use treatment status in our sampling design, but many of our 200 sites (n = 122, 61%) fell within a treatment area as determined using the NPS "Treatment" ArcGIS layer files, since sites with living, healthy hemlock were more likely to occur in treated areas. Treatment timing and success varied among sites, resulting in a continuum of hemlock decline rather than categorical hemlock retention versus total loss.

2.2. Vegetation surveys and hemlock decline index

We documented all living and dead hemlock trees within a 30-meter radius of the central point of each site. We assigned a size class on a scale of 0–4 to each hemlock by visually estimating the diameter at breast height (DBH) of each tree (Table 1). We similarly assigned each hemlock a rating on a health scale from 1 to 5 (Table 1), with 1 being a dead tree, and 5 being a live healthy tree, using the scale from Toenies et al. (2018). We excluded fallen trees that were moss covered or sufficiently decomposed that identification as hemlock could not be made with confidence. These trees were assumed to have been dead prior to the arrival of HWA and not applicable to this study.

Using the size and health class of each hemlock, we developed a site-level hemlock decline index, which was essentially the estimated amount of living and healthy hemlock basal area lost between eras. To calculate this index, we first estimated the pre-HWA hemlock basal area using the current-era live and dead hemlock tree data, as follows. We assumed that all observed individuals, regardless of current health, were alive and healthy during the pre-HWA era. We assigned each tree a mean DBH for its size class (Table 1) based on the assumption that it was within the same size class during the pre-HWA original surveys (Tingley et al., 2002). While some still-living individuals may have grown into a larger size class, we expect any bias to be negligible because hemlocks,

Table 1
Hemlock size class definitions and assigned average DBH for basal area estimations. Health class descriptions are from Toenies et al. (2018).

DBH size class	Observed DBH (cm)	Assigned DBH (cm)	Health class	Health scale factor	Description of health class
0	0 - 10	7	1	0.0	Complete mortality: fallen or still standing.
1	11 - 20	15	2	0.2	Severe limb die-off and needle loss, with live branches remaining along less than the top ⅓ of the tree.
2	21 - 35	28	3	0.4	Significant limb die-off and needle loss, but live branches remaining along the top ⅓ - ⅔ of the tree.
3	36 - 50	42	4	0.7	Minor limb die-off and needle loss, with live branches remaining along more than the top ⅔ of the tree.
4	> 50	60	5	1.0	Healthy, with no evidence of limb die-off or needle loss.

especially health-compromised individuals, are slow-growing. We then calculated pre-HWA total hemlock basal area (in m^2) within each site using the following formula (where DBH is in cm):

$$preHWA\ hemlock\ basal\ area_i = \sum_n^j \left((DBH_j/100)^2 \times \frac{\pi}{4} \right) \quad (1)$$

We calculated the health-adjusted post-HWA basal area for each tree by multiplying its basal area by its health scale factor (Table 1), then summed these within each site. The site-level Hemlock Decline Index (HDI; in units of m^2) was then calculated by subtracting the health-adjusted post-HWA hemlock basal area from the estimated pre-HWA basal area. We used the median HDI (~1.0) to split the 200 sites into low ($n = 101$) and high ($n = 99$) hemlock decline sites for some of the analyses below. (See Fig. S2 for examples of sites with low, medium, and high HDI indices.)

2.3. Avian point count surveys

We conducted 10-minute unlimited radius point counts (Reynolds et al., 1980) between sunrise and 10:00 a.m. (Ralph et al., 1995) from May 15 to June 30, 2018–2024, at 200 sites following the same protocol as Simons et al. (2006). We noted the presence of every bird detected by sight or by sound and whether it was within or beyond 50 m from the center of the point. Survey effort was comparable across eras: Simons et al. (2006) conducted 606 surveys across these 200 sites (average of 3.0 surveys per site), and the present study conducted 495 surveys across these same sites (average of 2.5 surveys per site).

2.4. Relative abundance analyses

From the replicated pre- and post-HWA era bird surveys, we created a relative abundance dataset of the maximum number of detections of each species within 50 m during any single visit at each site in each era (Rigby and Johnson, 2025), retaining all species that had ten or more detections in at least one era. We calculated site-level total abundance, species richness, and Shannon's Diversity Indices, comparing these between eras as a whole and between low and high hemlock decline sites. We used Wilcoxon signed-rank tests to measure changes in abundance for each species between eras, and quantified the effect of hemlock loss on relative changes in bird abundance using log response ratios (log RR; Hedges et al., 1999) for each species at each site as:

$$log\ RR = ln((N_t2 + 1)/(N_t1 + 1)) \quad (2)$$

where N_t1 and N_t2 are the abundances of a given species at a site during pre- and post-HWA survey periods, respectively. A pseudocount of 1 was added to all abundance values to allow log RR calculation in cases of zero observations. To estimate the effect of hemlock loss on each species' abundance change, we regressed log RR against the standardized (z-scored) HDI across all 200 sites separately for each species. The slope from each regression represents the direction and magnitude of a species' abundance response to hemlock loss, with negative slopes indicating decline at sites with greater hemlock loss, in units of log RR per standard deviation of the HDI. We calculated 90% confidence intervals around each slope estimate and considered a species' response to be directional when the confidence interval excluded zero. All analyses were conducted in R (R Core Team, 2025) using the tidyverse package (Wickham et al., 2019).

We applied PERMANOVA tests to evaluate the relationship between species composition and eras, and between estimated live hemlock basal area and species composition for each era separately. We used nonmetric multidimensional scaling (NMDS) ordination based on the Bray-Curtis index of species compositional dissimilarity to visualize site-level compositional differences between eras and to evaluate the contribution of individual species to the overall Bray-Curtis dissimilarities among sites, using the vegan package in R (Oksanen et al., 2025). Additionally, we used NMDS to assess whether healthy hemlock basal area was more strongly related to species composition in pre-HWA than in post-HWA. To test whether community differences between eras were related to hemlock decline, we used a *t*-test to compare low and high hemlock decline sites in terms of how much Bray-Curtis compositional change they showed between eras, and linear regression to test for a significant relationship between a site's hemlock decline index and Bray-Curtis dissimilarity between eras, after accounting for elevation as an explanatory variable.

2.5. Occupancy modeling

We modeled all species that were detected in at least 20 instances across both eras. We used single-species dynamic occupancy models to estimate initial occupancy (ψ), colonization (γ), and extinction (ε) probabilities in relation to hemlock covariates while accounting for imperfect detection (MacKenzie et al., 2003). Dynamic occupancy models assume that a species' occupancy state is constant within an era, using multiple visits per site in each era to estimate detection probability (p). ψ estimates the probability that a site was occupied during the pre-HWA sampling era; γ estimates the probability that an unoccupied site in the pre-HWA era became occupied in the post-HWA era; and ε estimates the probability that an occupied site became unoccupied (Kéry and Chandler, 2016). Dynamic occupancy models estimate ψ only for the initial era, so we also conducted a separate, single-season occupancy analysis for each species to evaluate the effect of post-HWA hemlock basal area on post-HWA occupancy. All occupancy models were built using the unmarked package in R (Fiske and Chandler, 2011).

2.5.1. Model fit and detection modeling

We assessed general model fit and estimated an overdispersion parameter (ĉ) for each species before evaluating the relative performance of different detection and occupancy covariates (Kelleher et al., 2025). To do so, we ran the global model: ψ(pre-HWA era hemlock basal area + elevation)γ(HDI)ϵ(HDI)p(minutes past sunrise + days past May 1). We performed the MacKenzie and Bailey goodness-of-fit test with 999 parametric bootstrap simulations, using functions in the R package AICcmodavg (Mazerolle, 2023; MacKenzie and Bailey, 2004). Throughout all subsequent analyses, we used ĉ to adjust standard errors for overdispersion. When $\hat{c} < 1$ (underdispersion), the value was adjusted to 1.0 following Burnham and Anderson (2002). As a result of the use of ĉ, all subsequent model selection used QAICc (quasi-AIC) as the model ranking criterion (Mazerolle, 2023).

To simplify analysis and minimize the number of models evaluated, we used model selection to first identify the top detection model for each species prior to evaluating site-level covariates on ψ, γ, and ε (Kéry et al., 2013; Jones et al., 2016). Four models, including an intercept-only model, were evaluated. Detection probability was modeled as a function of minutes past sunrise, days past May 1, or both (without interaction), while ψ, γ, and ε were held constant. Covariates included in the best-supported detection model (ΔQAICc = 0) for a given species were retained in all subsequent analyses for that species.

2.5.2. Assessing occupancy changes

Before evaluating the role of environmental covariates in driving occupancy changes, we wished to assess overall species-level changes in occupancy between eras. We therefore extracted bootstrapped estimates of ψ for both eras from the top detection model for each species using the nonparboot() function in unmarked, with 999 bootstrap replicates. Smoothed ψ estimates, standard errors, and 85% confidence intervals (following Arnold, 2010) were extracted for each era. We classified changes in ψ between eras as significant if their 85% confidence intervals did not overlap.

2.5.3. Site-level covariate effects

We used model selection and model-averaged parameter estimation to assess the influence of elevation, hemlock basal area, and HDI on ψ, γ,

and ε. Elevation was not a primary focus of the study, but it likely explained variation in the initial distribution of many species and was therefore included to better isolate hemlock associations and the effects of hemlock decline (Kelleher et al., 2025). We constructed a set of 16 candidate models, as follows. ψ was modeled using one of four formulas: a constant term, elevation, pre-HWA hemlock basal area, or both; γ and ε were each modeled with either a constant term or HDI (Table S1). We extracted model-averaged parameter estimates using the modavg() function in AICcmodavg (Mazerolle, 2023). Final estimates of coefficients on the standardized covariates were the weighted average across models, weighted by the model Akaike weights w_i (Burnham and Anderson, 2002). Covariates were standardized prior to analysis to facilitate model convergence and interpretation, and models that did not converge were removed from the model-averaging procedure.

We explored a treatment covariate in preliminary analyses, but treatment timing and success varied among sites, and the initial hemlock importance also varied within treatment polygons. As a result, a 1–0 categorical variable did not accurately represent the conditions in the field. To make our analysis biologically relevant for birds and to avoid overparameterizing our models, it was more informative to use a decline index. However, our analysis did allow for some post-hoc assessment of the impact of treatment.

3. Results

3.1. Changes to hemlock in GRSM

In total, we recorded 5823 hemlock trees within a 30 m radius of our 200 sites. Of these, 3320 hemlocks (57.0%) were dead, whereas 869 (14.9%) showed no sign of, or only minor, defoliation (Fig. 2A). The remaining 28.1% of trees were a mixture of moderate to severe defoliation. The largest size class had a greater proportion of dead trees than any other size class: of the 591 hemlocks with >50 cm DBH, 419 (70.9%) were dead. However, we found that percent mortality of hemlock at sites in treatment areas (57.3%) was significantly less than percent mortality at sites in untreated areas (73.1%; $t = -3.23$, $P = 0.0017$), and that sites with remaining hemlock tended to be in treated areas (Fig. 2B). Site-level HDI (estimated basal area of healthy hemlock loss between eras) ranged from 0 m^2 (no hemlock loss) to 7.2 m^2 (heavy hemlock loss), with a median of 0.98 m^2 (Fig. 2C).

3.2. Relative abundance analyses

Total bird abundance in the relative abundance data pre-HWA era was 1909 individuals across these 200 sites, and was 1446 birds post-HWA, an overall decrease of 24.3% in total abundance of birds over the study period. Site-level total abundance in post-HWA was less than in pre-HWA by 2.3 individuals ($t = 6.86$, $P < 0.001$, Fig. S3a), and differences were greater in high hemlock decline sites (3.4 fewer individuals over time, $t = 6.47$, $P < 0.001$) than in low hemlock decline sites (1.3 fewer individuals over time, $t = 3.13$, $P = 0.002$, Fig. S3b).

Overall species richness was similar between eras: after removing species with fewer than 10 detections in both eras, the pre-HWA relative abundance data contained 36 species and the post-HWA data contained 37 species. However, individual sites had 1.3 more species detected pre-HWA than post-HWA ($t = 5.29$, $P < 0.001$, Fig. S3c), and differences were greater in high hemlock-decline sites (1.8 more species in the pre-HWA era, $t = 5.03$, $P < 0.001$) than in the low hemlock-decline sites (0.7 more species in the pre-HWA era, $t = 2.35$, $P = 0.009$; Fig. S3d). Mean Shannon Diversity Index (H') for pre-HWA sites ($H' = 1.83$) was higher than the mean of post-HWA sites ($H' = 1.66$; $t = 3.94$, $p < 0.001$; Fig. S3e), and the mean difference was greater in high hemlock decline sites (pre-HWA $H' = 1.84$, post-HWA $H' = 1.64$, $t = 3.16$, $P = 0.002$) than in low hemlock decline sites (pre-HWA $H' = 1.81$, post-HWA $H' = 1.68$, $t = 2.36$, $P = 0.02$; Fig. S3f).

Wilcoxon signed-rank tests revealed 17 species that declined and 12 species that increased in relative abundance from the pre-HWA to the post-HWA era (Table 2), whereas log RR analysis revealed 13 species whose relative abundance declined and five species whose relative abundance increased with increased hemlock loss (Fig. 3). Not all species with relative abundance changes due to hemlock loss had significant abundance changes overall between eras, and not all significant changes in abundance between eras were due to hemlock loss. For example, Scarlet Tanager did not significantly decline from the pre-HWA to the

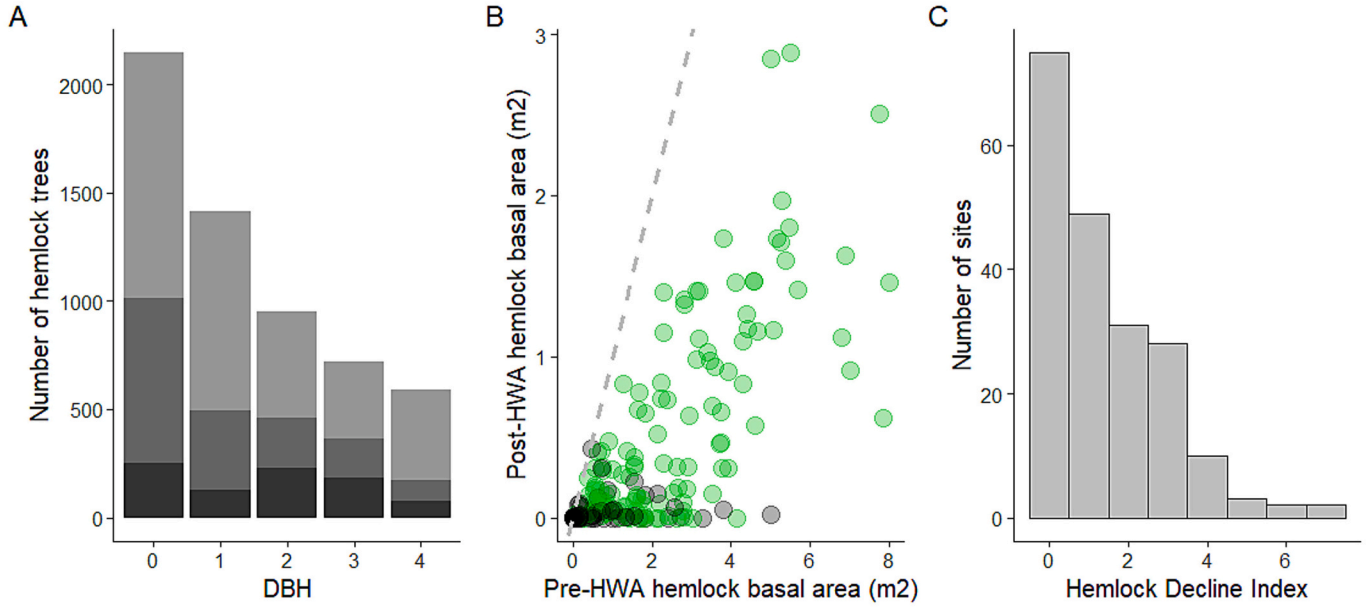


Fig. 2. A) The number of post-HWA hemlock trees in each DBH category and health category (see Table 1). Light gray = dead; medium gray = moderate to severe defoliation; black = healthy to mild defoliation. B) Estimated hemlock basal area pre-HWA vs. health-adjusted post-HWA basal area, colored according to whether a site was within (green) or outside (gray) HWA treatment areas. Gray dashed 1:1 line shows where pre-HWA basal area = post-HWA basal area. C) Histogram of the Hemlock Decline Index, the estimated site-level decrease in healthy hemlock basal area from pre- to post-HWA eras. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2
Relative abundance across all sites of 37 species with >=10 detections in at least one era, with change (delta) and Wilcoxon signed-rank test *P*-values between pre- and post-HWA eras.

Species included in analysis			Relative abundance			Wilcoxon *P*-value
Common name	Scientific name	4-Letter code	Pre-HWA	Post-HWA	Delta	
Acadian Flycatcher	*Empidonax virescens*	ACFL	76	22	−54	0.000
American Crow	*Corvus brachyrhynchos*	AMCR	4	29	25	0.002
American Robin	*Turdus migratorius*	AMRO	8	20	12	0.040
Black-and-White Warbler	*Mniotilta varia*	BAWW	81	59	−22	0.024
Blackburnian Warbler	*Setophaga fusca*	BLBW	51	21	−30	0.000
Black-capped Chickadee	*Poecile atricapillus*	BCCH	29	12	−17	0.014
Black-throated Blue Warbler	*Setophaga caerulescens*	BTBW	198	79	−119	0.000
Black-throated Green Warbler	*Setophaga virens*	BTNW	186	137	−49	0.002
Blue Jay	*Cyanocitta cristata*	BLJA	5	16	11	0.029
Blue-headed Vireo	*Vireo solitarius*	BHVI	136	107	−29	0.031
Brown Creeper	*Certhia americana*	BRCR	23	31	8	0.365
Canada Warbler	*Cardellina canadensis*	CAWA	24	10	−14	0.006
Carolina Chickadee	*Poecile carolinensis*	CACH	25	26	1	0.853
Carolina Wren	*Thryothorus ludovicianus*	CARW	9	29	20	0.001
Chimney Swift	*Chaetura pelagica*	CHSW	3	38	35	0.000
Dark-eyed Junco	*Junco hyemalis*	DEJU	110	45	−65	0.000
Downy Woodpecker	*Dryobates pubescens*	DOWO	11	16	5	0.361
Eastern Towhee	*Pipilo erythrophthalmus*	EATO	10	35	25	0.000
Golden-crowned Kinglet	*Regulus satrapa*	GCKI	72	10	−62	0.000
Hairy Woodpecker	*Dryobates villosus*	HAWO	18	20	2	0.724
Hooded Warbler	*Setophaga citrina*	HOWA	88	135	47	0.000
Indigo Bunting	*Passerina cyanea*	INBU	14	3	−11	0.015
Northern Cardinal	*Cardinalis cardinalis*	NOCA	2	29	27	0.000
Northern Parula	*Setophaga americana*	NOPA	52	57	5	0.553
Ovenbird	*Seiurus aurocapilla*	OVEN	172	81	−91	0.000
Pileated Woodpecker	*Dryocopus pileatus*	PIWO	9	23	14	0.014
Red-breasted Nuthatch	*Sitta canadensis*	RBNU	23	16	−7	0.227
Red-eyed Vireo	*Vireo olivaceus*	REVI	210	104	−106	0.000
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	RBGR	14	1	−13	0.006
Scarlet Tanager	*Piranga olivacea*	SCTA	67	54	−13	0.185
Swainson's Warbler	*Limnothlypis swainsonii*	SWWA	0	35	35	0.000
Tufted Titmouse	*Baeolophus bicolor*	TUTI	18	37	19	0.018
Veery	*Catharus fuscescens*	VEER	48	20	−28	0.000
White-breasted Nuthatch	*Sitta carolinensis*	WBNU	15	30	15	0.017
Winter Wren	*Troglodytes hiemalis*	WIWR	49	15	−34	0.000
Wood Thrush	*Hylocichla mustelina*	WOTH	27	15	−12	0.046
Worm-eating Warbler	*Helmitheros vermivorum*	WEWA	22	29	7	0.291

post-HWA era (Table 2) but did significantly decline as HDI increased (Fig. 3), and Brown Creeper did not significantly increase from pre-HWA to post-HWA (Table 2) but did significantly increase as HDI increased (Fig. 3). American Robin increased significantly from pre-HWA to post-HWA (Table 2) but this was not related to HDI (Fig. 3). Interestingly, both Red-eyed Vireo and Indigo Bunting decreased significantly from pre-HWA to post-HWA but tended to increase at sites with higher hemlock loss (Fig. 3).

PERMANOVA tests revealed a significant difference between pre- and post-HWA bird community composition as a whole ($P = 0.001$) and suggested that live hemlock basal area was more strongly related to species composition pre-HWA ($P = 0.0001$) than it was post-HWA ($P = 0.002$). NMDS helped to visualize these differences (Fig. 4) and revealed which species most influence species composition in both communities as a whole (Fig. 4a) and separately in each era (Fig. 4c and d). Fewer species appear to be associated with hemlock basal area in the post-HWA era, and these are different species than in the pre-HWA era (Fig. 4d). Mean Bray-Curtis dissimilarity between pre- and post-HWA in low hemlock decline sites was 0.661 (95% CI [0.635, 0.687]) and at high hemlock decline sites was 0.687 (95% CI [0.661, 0.713]), and there was no difference in era mean dissimilarity between those site types ($t = -1.39$, $P = 0.164$). Linear regression revealed no significant relationship between HDI and dissimilarity ($F = 7.615$, $P = 0.179$; Fig. 4b) after accounting for elevation.

3.3. Occupancy results

In total, 35 species met the threshold of at least 20 detections across both eras and were included in subsequent analyses. After running the goodness-of-fit test on the global model for each species, the average $\hat{C}$ was 1.33, just above the ideal value of 1 (Burnham and Anderson, 2002). The null detection model was the best fit for 12 species, suggesting no strong influence of time-related covariates on detection probability for those species (Table S2). For others, detection varied with the date or with the time of day. We then moved the top detection formula for each species down to all subsequent analyses.

According to our dynamic occupancy analysis, seven species declined in occupancy between the pre-HWA and post-HWA eras: Acadian Flycatcher, Black-throated Blue Warbler, Dark-eyed Junco, Golden-crowned Kinglet, Red-eyed Vireo, Ovenbird, and Winter Wren (Fig. S4; Table S3). Acadian Flycatcher, one of the focal species of our study, occupied 42% of sites during the pre-HWA era ($\psi = 0.42$; 85% CI: 0.32–0.52) but occupied only 18% of sites during the post-HWA era ($\psi = 0.18$; 85% CI: 0.12–0.25). In contrast, seven others showed a significant increase in occupancy between the pre- and post-HWA eras, including Carolina Wren, Eastern Towhee and Hooded Warbler. Notably, Swainson's Warbler was absent in the pre-HWA era but showed a moderate post-HWA occupancy estimate ($\psi = 0.31$; 85% CI: 0.11–0.50).

3.3.1. Effects of hemlock and elevation on pre-HWA occupancy

After incorporating site-level covariates, elevation was an important occupancy predictor for more than half of the species in our analysis (Table S4). For example, Canada Warbler, Winter Wren, and Blackburnian Warbler all exhibited higher occupancy probabilities at higher elevations.

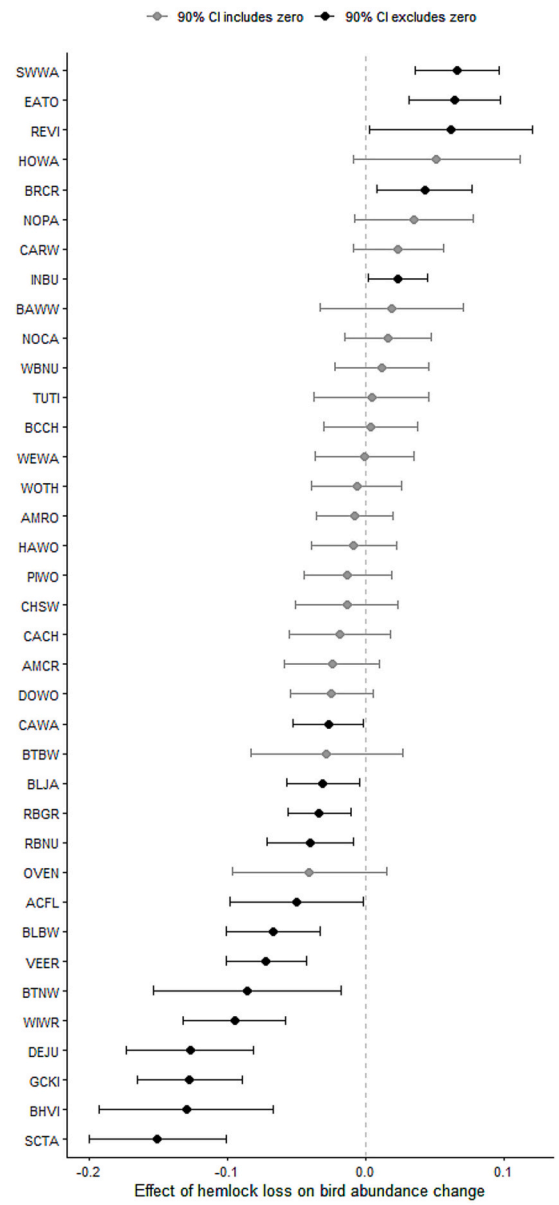


Fig. 3. Log RR-calculated effect sizes (with 90% CIs) of the impact of HDI on bird species relative abundance changes. Species 4-letter codes are labeled as in Table 2. Negative slopes indicate a decline in species relative abundance due to hemlock decline, and black data points are species whose 90% CIs do not cross zero.

Pre-HWA hemlock basal area also influenced occupancy for 12 species (Table S4). Seven of these species exhibited significantly positive relationships, with higher pre-HWA occupancy at sites with higher hemlock basal area. These species included Acadian Flycatcher (Fig. 5a), Black-throated Blue Warbler (Fig. 5b), Black-throated Green Warbler (Fig. 5c), Dark-eyed Junco, Golden-crowned Kinglet, Veery (Fig. 5d), and Winter Wren. In contrast, results from the single-season occupancy analysis examining the relationship between post-HWA hemlock basal area and post-HWA occupancy indicated a substantial decline in positive associations. The number of species positively associated with hemlock basal area decreased from seven to two, Black-throated Green Warbler (Fig. 5c) and Swainson's Warbler (Table S5).

3.3.2. *Extinction and colonization probabilities*

Three species, Ovenbird (Fig. S5), Veery, and Scarlet Tanager, displayed a positive relationship between the HDI and extinction probability. This indicates that, among sites occupied by these species prior to HWA introduction, those with greater hemlock loss were more likely to lose these species. In contrast, Winter Wren, Black-throated Blue Warbler (Fig. S5), and Canada Warbler exhibited the opposite pattern; their extinction probability decreased as hemlock decline intensified, suggesting these species were more likely to persist at sites with greater hemlock loss compared to other sites. Brown Creeper, Swainson's Warbler, and Eastern Towhee also responded positively to the HDI, showing higher colonization probabilities at sites with greater hemlock loss, with confidence intervals that did not include zero. Blue Jay and Pileated Woodpecker displayed a negative relationship between colonization probability and the HDI, although the confidence intervals indicate uncertainty in these estimates (Table S4).

4. Discussion

We measured changes to bird species abundances, diversity, and occupancy patterns in GRSM after 25 years of HWA invasion and subsequent hemlock loss. Across 200 sites in GRSM, we found fewer individuals, fewer species, and lower community diversity compared to surveys performed pre-HWA, and these differences were greater at sites with high hemlock loss. The influence of this foundation species on the structure and composition of avian communities decreased following the arrival of HWA, with fewer species' relative abundance patterns aligning with healthy hemlock basal area and less variation in species community composition explained by hemlock presence. Although observational studies such as this cannot definitively assign hemlock loss as the primary cause of these changes (Larsen et al., 2019), the comparison of pre- and post-decline data at individual sites strengthens our conclusions, and these results are in line with our initial hypotheses and with findings from across the range of HWA infestation.

Similar to several studies across the hemlock's range (Tingley et al., 2002; Ross et al., 2004; Becker et al., 2008) and in line with our hypotheses, we documented abundance declines of hemlock-associated birds including Acadian Flycatcher, Black-throated Green Warbler, and Blue-headed Vireo in GRSM since the arrival of HWA (Fig. 6, Table 2). Unlike other studies however, we documented hemlock-related declines in Winter Wren, Canada Warbler, and Dark-eyed Junco, which are considered “trailing-edge” species in the southern Appalachians (Gaya and Chandler, 2025). Together with the wide range of avian responses reported across studies (Fig. 6), these results suggest that bird-hemlock associations and responses to hemlock loss differ across hemlock's range (Amaral et al., 2023). Compared to northeastern forests, southern Appalachian forests generally had lower pre-HWA hemlock densities (Whittaker, 1956; Block et al., 2012) and have greater floristic diversity (Manos and Meireles, 2015), potentially weakening bird-hemlock relationships. Further, the elevational range that hemlock spans in GRSM may allow for different species associations here than further north, leading to differences in avian responses to hemlock loss. Forest succession following hemlock loss also differs. Rhododendron and other dense understory growth is more common after hemlock decline in the southern Appalachians (Ford et al., 2012), while hardwood regeneration is more common in the northeastern portion of its range.

As a disturbance event, hemlock loss alters forest structure, typically resulting in a more open canopy and increased shrub and sapling density in the understory in the Southern Appalachians (Vose et al., 2013; Ford et al., 2012). Although we did not quantify loss of open understory or closed canopy in this study, changes to the forest floor can be expected to negatively impact species that rely on an open understory for nesting and foraging. Our results showing declines in Ovenbird (similar to Tingley et al., 2002) reflect this, as this species nests and forages in open understory (Canterbury and Blockstein, 1997). Similarly, the canopy-associated Scarlet Tanager (Mowbray, 2020) likely declined in response to increased canopy gaps common in high hemlock-decline sites, despite this species not being typically associated with hemlocks

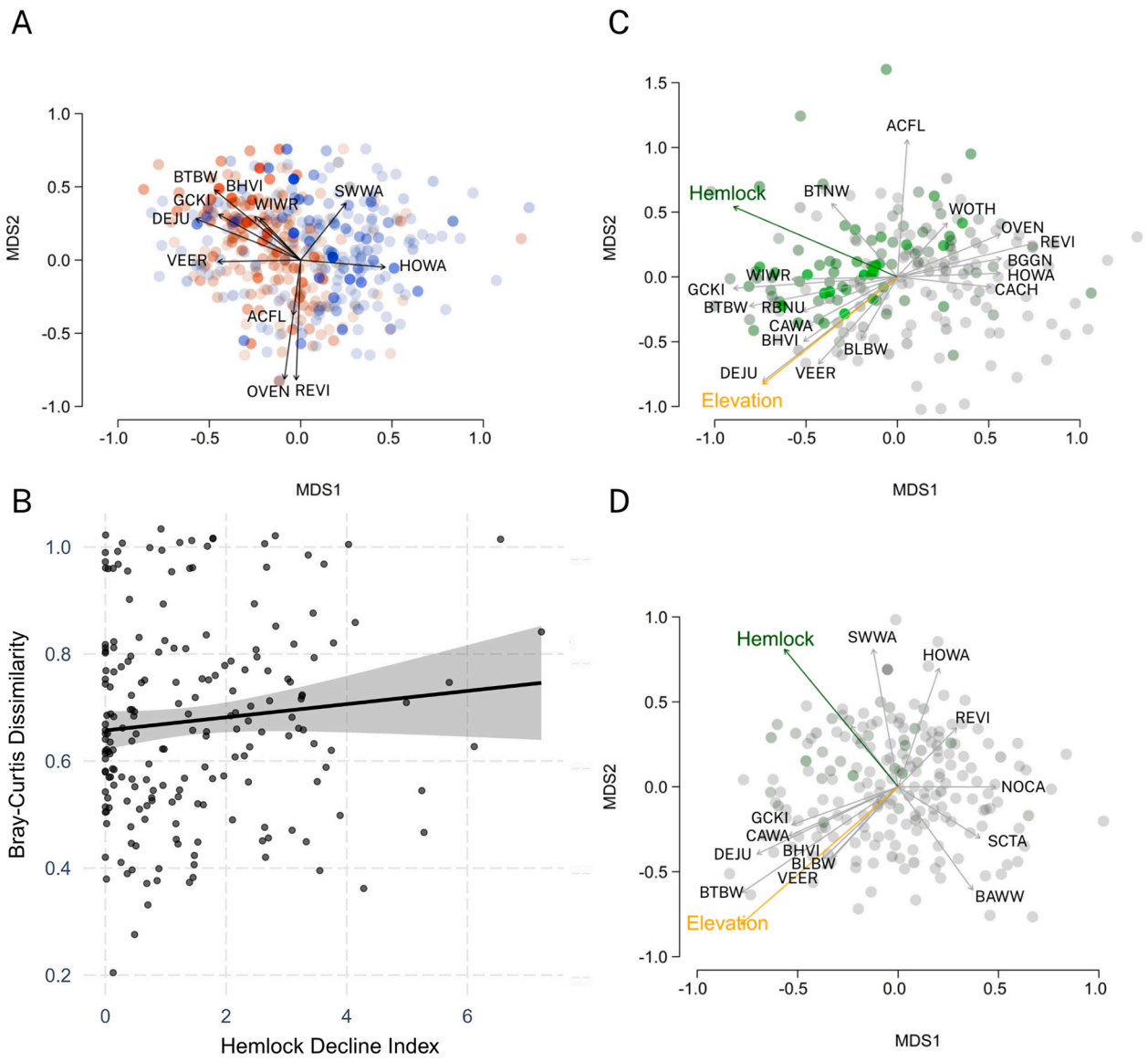


Fig. 4. Results of NMDS and Bray-Curtis dissimilarity tests. A. Both eras combined, circles are sites color-coded according to era (pre-HWA = red, post-HWA = blue) and filled according to estimated healthy hemlock basal area. Bird species overlaid are those that strongly impact community composition across both eras, and 4-letter code abbreviations are as in Table 2. B. Linear regression and fit line showing nonsignificant relationship between HDI and Bray-Curtis dissimilarity after accounting for elevation. C. NMDS for pre-HWA only, sites filled according to estimated healthy hemlock basal area, with species that most strongly influenced community composition and their relationship to both hemlock basal area (green arrow) and elevation (yellow arrow). D. Same plot as C but for the post-HWA era. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

elsewhere (Fig. 6).

Although we did not quantify non-hemlock vegetation structure, disturbed and open canopy areas with dense understory including abundant rhododendron were typical at our high hemlock-decline sites. Our results for Eastern Towhee, Northern Cardinal, and Swainson's Warbler align with our hypothesis that these structural changes benefit early successional, disturbance-dependent, and shrub associated species (Billerman et al., 2026). Similarly, increases in Brown Creeper may be due to increased nesting habitat in dead hemlock trees with peeling bark (Poulin et al., 2020). None of these four species responded positively to hemlock decline in other studies (Fig. 6), further signaling geographic variation in bird responses to hemlock decline.

Disturbance-dependent species are declining across much of eastern North America (NACBI, 2025), largely due to a maturing forest canopy and lack of widespread disturbance or forest management practices that are beneficial to these species. Localized disturbances can lead to increases in some species, especially where such disturbances are severe, highlighting the fact that localized abundance shifts can be in the opposite direction of continental-scale trends (Johnston et al., 2025). Greenberg et al. (2023) documented increases in total abundance and richness of breeding birds following high-severity wildfires in the southern Appalachians in 2016, including increases in disturbance-dependent birds. We found similar increases in some disturbance-associated species but did not see increases in total abundance or richness of breeding birds, suggesting that hemlock loss following HWA invasion is not as severe a disturbance event as large-scale wildfires.

Winter Wren, Black-throated Blue Warbler, and Canada Warbler all significantly declined in relative abundance across the 25-year time period (Table 2). However, their extinction probabilities were lower at sites with high HDI (Table S4), which included sites with some intact hemlock basal area. One explanation is that these species responded positively to similar habitat characteristics as the disturbance-associated species. Black-throated Blue Warbler and Canada Warbler both associate with dense forest understory, and Winter Wren forages and nests in

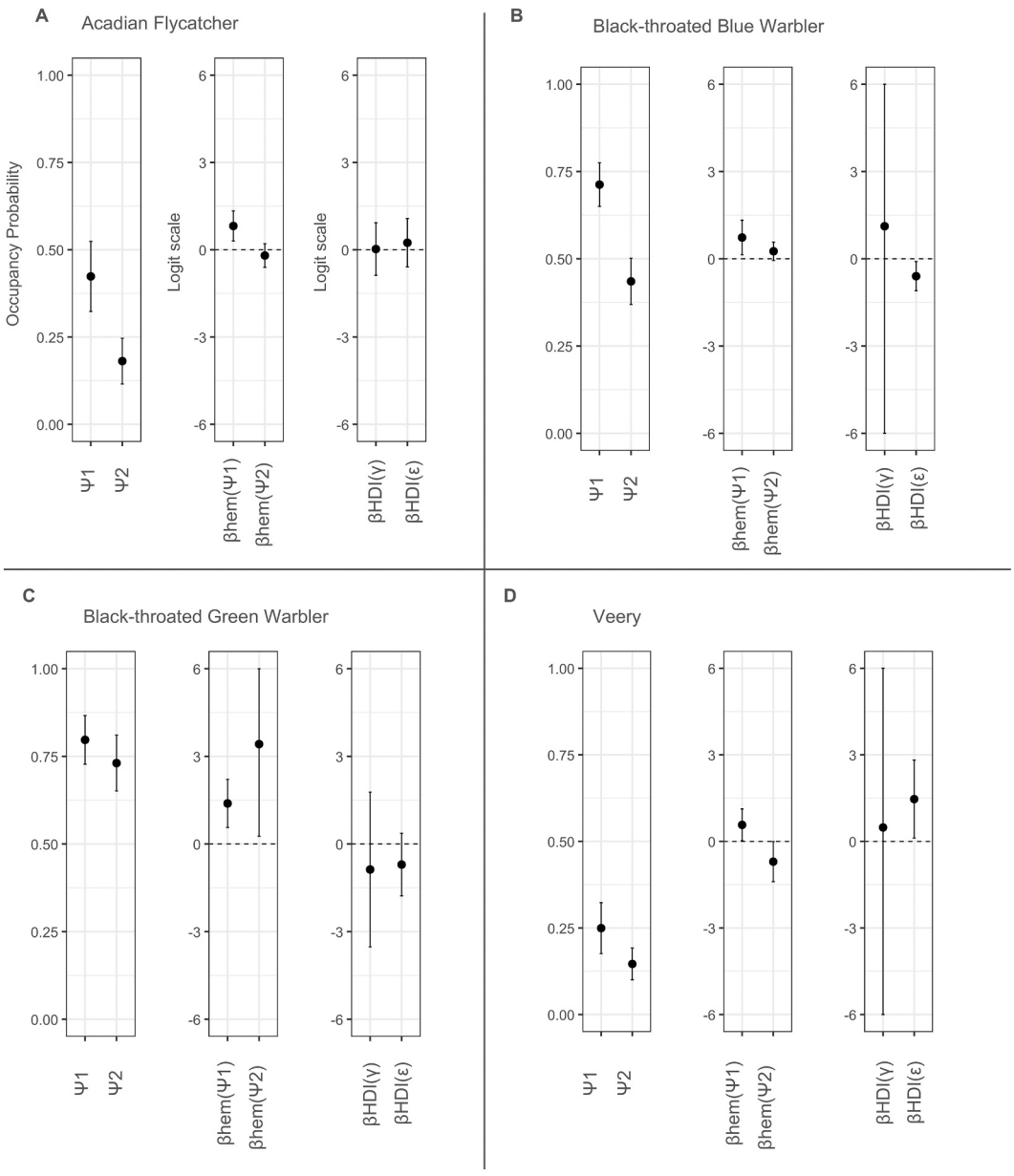


Fig. 5. Model-averaged estimates and 85% confidence intervals from dynamic occupancy models for selected species. Panels show estimated occupancy probability in the pre- and post-HWA eras (left); effects of pre- and post-HWA hemlock basal area on initial occupancy for pre- and post-HWA eras (middle); and effects of HDI on colonization and extinction parameters (right). Estimates for occupancy are probabilities, while covariate effects are shown on the logit scale. The effect of hemlock basal area on post-HWA occupancy is not from a model-averaged approach and is instead a single-season analysis due to the constraints of dynamic occupancy modeling. For a full species list of these results, see Tables S3-5.

downed and standing dead wood substrates (Billerman et al., 2026). Alternatively, the remaining hemlock may still provide sufficient nesting and foraging opportunities; all three species showed positive relationships with pre-HWA hemlock basal area. The process of hemlock decline may create disturbance-associated habitat while still retaining enough hemlock structure to support some hemlock-associated birds (Toenies et al., 2018), a situation that we observed at some of our study sites.

The changes in these bird communities during this study period occur in the context of global change, with some changes in abundance clearly caused by hemlock loss and others following larger-scale trends in their populations. We found that overall forest bird abundance in GRSM has declined by nearly 25% since the late 1990s, largely due to major abundance decreases in migratory forest species such as Black-throated Blue Warbler, Red-eyed Vireo, and Ovenbird. These trends are consistent with the 17% (Rosenberg et al., 2019) and 27% (NABCI, 2025) declines in eastern North American forest birds since 1970 documented elsewhere. We also found abundance and occupancy declines in high-elevation species that reach their southern distributional range limit here ("trailing-edge" species) including Dark-eyed Junco, Golden-crowned Kinglet, and Winter Wren, consistent with recent results from this trailing-edge hotspot of the southern Appalachians (Gaya and Chandler, 2025).

To our knowledge, our study is the first community-level investigation of bird responses to hemlock decline in the southern Appalachian region but is not the first study in GRSM to identify potential wildlife benefits associated with hemlock conservation and treatment (Cox et al., 2022). Falcone and DeWald (2010) linked higher bird density of three focal species to increased hemlock foliage mass, suggesting that sites with better hemlock health can support greater numbers of birds, similar to our results (Fig. S3A). Together, these results suggest that continued

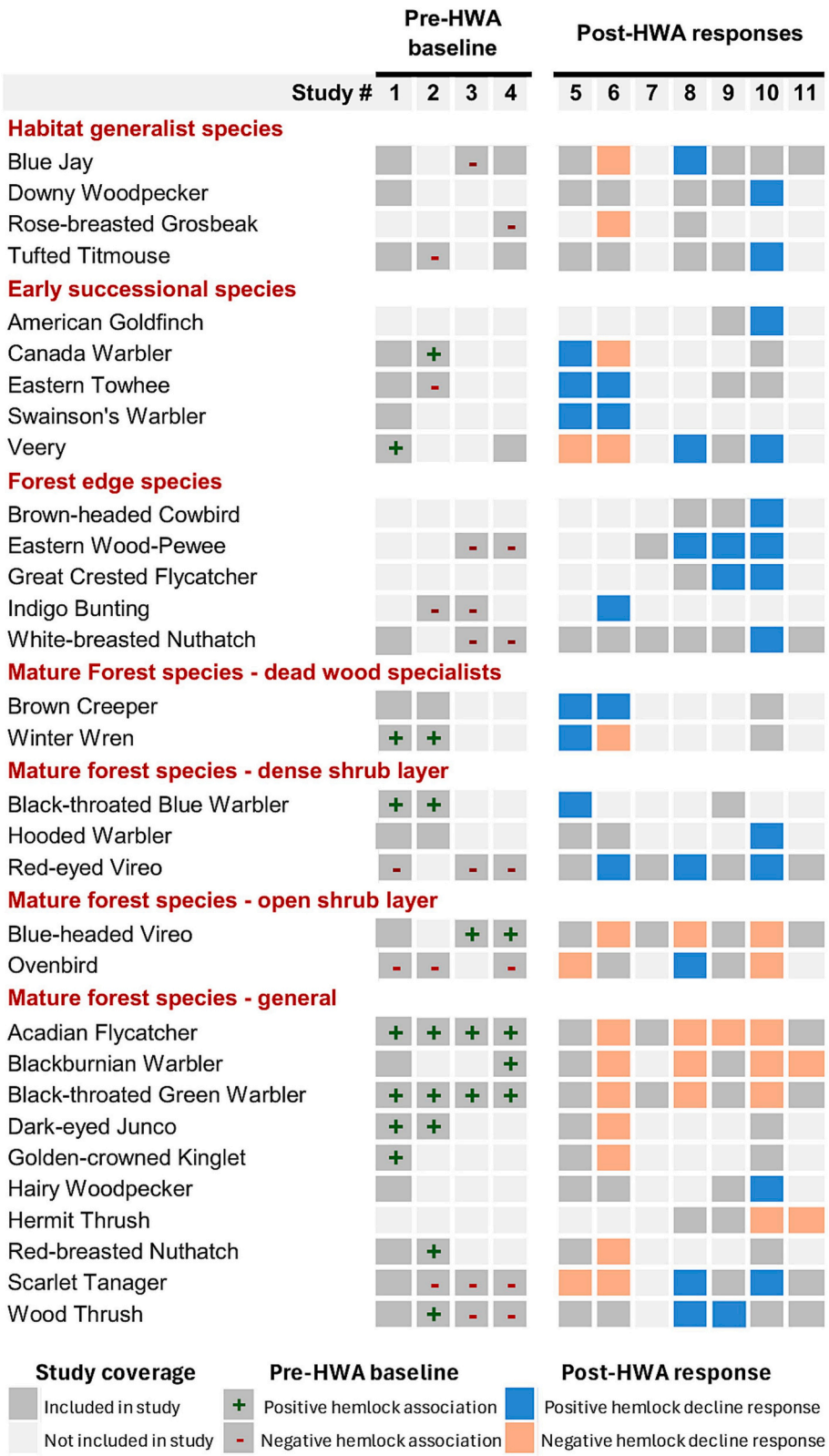


Fig. 6. Review of species' associations with pre-HWA hemlock and responses to post-HWA hemlock decline. Species included are all those with a significant response to hemlock decline in any of the post-HWA studies listed, including this current study. Habitat categories were derived from the "Habitat in Breeding Range" subsection of *Birds of the World* (Billerman et al., 2026). Within each HWA era, studies are arranged from lowest to highest latitude.
[1]Current study (occupancy results), [2]Shriner (2001), [3]Brown and Weinkam (2014), [4]Ross et al. (2004), [5]Current study (occupancy), [6]Current study (relative abundance), [7]Bekins and Brown (2022), [8]Toenies et al. (2018), [9]Becker et al. (2008), [10]Tingley et al. (2002), [11]Amaral et al. (2023). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

loss of hemlock may have important conservation impacts for a subset of bird species. For species with strong evidence of hemlock association across multiple studies—including Acadian Flycatcher, Black-throated Green Warbler, Blackburnian Warbler, and Blue-headed Vireo—these consequences may increase as climate change expands the distribution and impacts of HWA (McAvoy et al., 2017; Thomas and Orwig, 2025).

In GRSM, despite widespread mortality from HWA, hemlock remains an important component of forests, with over 40% of hemlocks recorded in this study still alive. Mortality was significantly lower in treated areas, maintaining a continuum of hemlock decline severity throughout the study area. For these reasons, GRSM represents an ideal venue for future studies examining the mechanistic relationships between birds and their use of remnant hemlock in the landscape, including nesting and foraging behaviors. This study identified correlational relationships between bird species and hemlock; follow-up studies in the region should consider threshold analyses to determine how many hemlock trees managers should maintain on the landscape to support these more-vulnerable species.

Our results suggest that the avian conservation and management implications of hemlock decline may vary across the species' range, reflecting differences in both hemlock's initial importance and forest succession following its loss. We found increases in disturbance- and shrub-associated species that are species of conservation concern potentially due to distinctive post-HWA forest succession in this part of the hemlock range. Managers in the southern Appalachians may consider supporting small-scale forest disturbance processes while also protecting remaining hemlock conservation areas. Where HWA has caused extensive mortality among untreated hemlocks, conservation areas may be especially important for species repeatedly identified as hemlock-associates across studies, including Acadian Flycatcher, Black-throated Green Warbler, Blackburnian Warbler, and Blue-headed Vireo. Emerging methods to conserve hemlock in the southern Appalachians also include creating small clearings around hemlocks, an approach that can improve hemlock health through greater available sunlight while also providing habitat for disturbance-dependent forest wildlife (Mayfield et al., 2026).

5. Conclusion

We documented changes to forest bird communities following 25 years of HWA infestation and subsequent hemlock decline in the southern Appalachian Mountains, including overall lower abundance and diversity of birds, a loss of community compositional structuring by hemlock, and changes in site occupancy at the species level associated with vegetation change. Some of these results differed from bird-hemlock studies conducted in more northern portions of the hemlock range, suggesting geographic variation in bird-hemlock associations and regionally variable impacts of hemlock loss. Locally appropriate forest bird habitat management recommendations in the wake of hemlock decline are therefore likely to benefit from attention to this regional variability.

CRediT authorship contribution statement

Ally J. Melrose: Writing – original draft, Visualization, Investigation, Formal analysis, Conceptualization, Methodology. **Nicole M. Mooradian:** Writing – original draft, Investigation, Conceptualization. **Lars Y. Pomara:** Writing – review & editing, Investigation, Formal analysis, Conceptualization. **Andrew J. Laughlin:** Writing – original draft, Project administration, Methodology, Investigation, Formal analysis, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used ChatGPT (OpenAI, GPT-5.5) to suggest potential methods for the analysis and representation of effect size of hemlock decline on relative abundance and to assist with writing loops to automate occupancy analyses. After using these tools, the authors reviewed, verified, and modified the content as needed and take full responsibility for the content of the published article. All analyses were performed within R.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2026.112183.

Data availability

Historical data from Shriner (2001) are unavailable for sharing. Post-HWA data are part of ongoing analyses but may be available from the corresponding author upon reasonable request. Code available on Zenodo (DOI: https://doi.org/10.5281/zenodo.23888174)

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